

Determination of Asymptotic Growth in Progenies of Crosses Between *Clarias gariepinus* and *Heterobranchus longifilis* and Attenuation of Intra-cohort Cannibalism

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Abstract

Using weight as a measure of size in cannibalistic species can be misleading. This research determined the growth pattern, cannibalism and heterosis of crosses between two African catfishes *Clarias gariepinus* (Cl) and *Heterobranchus longifilis* (Ht). Fry were reared communally for Cl×Cl, Cl×Ht, Ht×Cl and Ht×Ht for 14 days before triplicates of 100 fry were randomly stocked in concrete ponds. The length of the samples was taken weekly, and growth shooters were sorted out using the criteria of cut-off length earlier proposed by the authors. The Gompertz model successfully converged for the growth modelling of three crosses: Cl×Cl, Cl×Ht and Ht×Cl with asymptotic values of 40.44 mm, 59.42 mm, 57.27 mm. In contrast, the cross Ht×Ht converged using the monomolecular growth model with an asymptotic length of 72.09 mm. Type I and type II cannibalism were observed with a greater influence of *H. longifilis*. Absolute growth rate (AGR) was highest in Ht×Cl (1.52 mm.day⁻¹) progeny and lowest in Ht×Ht (1.02 mm.day⁻¹). There was positive heterosis for length and AGR with negative heterosis for survival (-8.93%) and sorting (-1.86%). There was positive heterosis for cannibalism. The study revealed the maximum length attainable for offspring of these crosses and sorting effectiveness/criteria.

Introduction

The concept of growth is utilized in fisheries management to control the three basic factors in fish population dynamics: recruitment, biomass increase (individual or collective) and mortality. Growth is an important factor in aquaculture, and it is simply expressed as an increase or addition of biomass in the entire population or for each fish. In fish genetics, growth is a desirable quantitative trait sought after by breeders and geneticists. Attempts have been made to increase growth in the African catfish as well as other fish species by crossbreeding via intra-specific

(Wachirachaikarn et al., 2009), interspecific (Chaivichoo et al., 2020), and inter-generic (Ataguba et al., 2010) crosses. In our earlier report on the growth performance of crosses between *Clarias gariepinus* and *Heterobranchus longifilis*, we presented a small heterosis for growth in fry but a negative heterosis for their survival. In contrast, fingerling growth had a substantial negative heterosis for growth and a positive heterosis for survival. These results indicate that crossbreeding elicits more remarkable survival, but it comes at a price of reduced growth.

In aquaculture, growth is tied to stocking density (Abou et al., 2007) and the carrying capacity of the

culture system (Ferreira et al., 2013). The gross yields of the African catfish *C. gariepinus* have been reported to be better at high stocking density than at low stocking density (Hengsawat et al., 1997). The benefit of high stocking density in aquaculture of the African catfish will therefore be increased earnings (Oké & Goosen, 2019; Shoko et al., 2016). As stocking density increases, there is bound to be a limit to which the culture system or facility can take. Hence, the concept of carrying capacity. The area under cultivation and the number of fish stocked, are determined by the availability of farm structures and appropriate planning to ensure sustainable production (Salin & Ataguba, 2018). Accordingly, carrying capacities can be modelled using water quality standards and biomass loading on the farm (Stigebrandt, 2011).

However, biological growth limits determine pond or tank level stocking density for optimal yield in individual growth that will also translate to total harvest. Studies have focused on the effects of stocking density on yield, with a direct relationship (Hengsawat et al., 1997; M'balaka et al., 2012; Oké & Goosen, 2019; Shoko et al., 2016). This is the concept of production carrying capacity, and it is a function of stocking density as a determinant of optimal harvest (Byron, 2010). The determination of growth rates in aquaculture relies on the specific growth rate (SGR). However, a recent review by Crane et al. (2019) highlighted a major flaw in the determination of SGR. They indicated that values reported using the linearized exponential growth function were dimensionless. Therefore, the value obtained must be used as power to raise the Euler's number and subtract one before multiplying by 100 to give SGR in $\% \cdot \text{day}^{-1}$. Although the exponential growth function is ideal for the fast growth phase, it is weak when there is a need to determine an asymptote (highest achievable growth in the system). The function is limited because the asymptote is not included in the model and would have to be determined separately. Unfortunately, size variability is very high in the early phase of fish growth (Terhune et al., 1997), which does not allow for greater accuracy in carrying capacity.

Size variation is linked directly to stocking density, such that high stocking densities elicit greater size variation among fish (Terhune et al., 1997). According to Dasuki et al. (2013), there was a greater standard error in final weight of *C. gariepinus* reared at higher stocking densities than the lowest stocking density. Furthermore, size variability is common among cohorts of offspring from the same parental lines. As a result of size variation and the need for frequent sorting, there is a plethora of research into the frequency of sorting and its effect on growth with varied recommendations, including twice a week (Maradun et al., 2019) and every fortnight (Oyoo-Okoth et al., 2020).

The growth pattern of the African catfishes *C. gariepinus* and *H. longifilis* is allometric such that size and growth potential increase in tandem until growth is no longer possible (van Denderen et al., 2019). Size

heterogeneity in a culture facility affects growth performance (Baras & Fortuné dAlmeida, 2001). Size heterogeneity also leads to increased cannibalism within the culture units (Obirikorang et al., 2014). According to Baras and Jobling (2002), cannibalism will peak within the first few weeks or months of cultivation before levelling off at the point where size heterogeneity ceases to exist because individuals reach optimal size. Aggressive behaviour tends to come with size heterogeneity as larger fish bully smaller ones and end up cannibalizing them (Naumowicz et al., 2017) and this will reduce production. From the foregoing, this research will determine the asymptotic length and show the dynamics of size variation and cannibalism in both pure line and reciprocal crosses of the two African catfishes.

Materials and methods

Fish

Broodstock of the two African catfish species were obtained from the University of Agriculture Makurdi fish farm and maintained in concrete tanks with males and females being held separately. A total of six broodstock (Table 1) comprising two females each and a male each of *C. gariepinus* (Cl) and *H. longifilis* (Ht) were obtained. The weight of the female broodstock (Table 1) ranged from 800g to 1200g, while the weight of the male broodstock were 900g and 1000g each.

Induced Breeding

Oocyte maturation and ovulation was induced by a single intramuscular injection of Ovaprim (0.5 ml kg^{-1}) (Table 1). After the injection of hormones, male and female fish were kept separately to prevent natural spawning and aggressiveness. The time between injection and ovulation was 12 and 15 hours for *C. gariepinus* and *H. longifilis*, respectively. After ovulation, eggs were collected by manually pressing the abdomen toward the caudal fin into a dry clean plastic bowl. A single male was used to fertilize eggs for two different crosses as required (one lobe of testes in each case). Milt collection and fertilization were carried out using the method previously described by Ataguba et al., (2010). The fertilized eggs were incubated in 60L plastic aquaria in each case. Incubation was done using a static water system with constant aeration. The mating combination used for the experiment (Table 2) was the reciprocal crossing system to elicit maternal effects in performance for growth and size heterogeneity.

Experimental Design

Upon hatching, fry was nursed in four concrete tanks ($2 \text{ m} \times 1 \text{ m} \times 1 \text{ m}$) for two weeks and fed with artemia before being weaned to a starter diet. Feeding was *ad libitum*. On the 15th day, fry was collected from

Table 1. Weight and volume of hormone for induced breeding of reciprocal crosses.

Species	Female		Male
	Weight (g)	Hormone (ml)	Weight (g)
<i>C. gariepinus</i>	1100	0.055	1000
	1200	0.06	
<i>H. longifilis</i>	800	0.04	900
	1000	0.05	

Table 2. Punnet’s square for reciprocal crosses between *C. gariepinus* and *H. longifilis*.

		♂	
		Cl	Ht
♀	Cl	Cl×Cl	Cl×Ht
	Ht	Ht×Cl	Ht×Ht

the nursing tanks in triplicate batches of 100 and placed in concrete tanks (1 m×1 m×1 m) to give a stocking density of 100 fish.m⁻². Mean initial lengths of fish from each cross include: 17.99mm (Cl×Cl), 19.36 mm (Cl×Ht), 19.08 mm (Ht×Cl) and 12.72 mm (Ht×Ht). The water level was maintained at 0.6 m hence a water volume of 600 L. Water exchange (99%) was carried out every week. Feeding was done at a frequency of two times daily *ad libitum* to ensure every fish had some feed to eat. Data collected includes length, cannibalism, and water quality parameters every week. Length was measured using a ruler graduated in millimetres while water quality was determined using various methods. Water quality parameters, including pH and Dissolved Oxygen of the water were monitored using Hanna Multiparameter Water Quality Probe Model HI-98129. A mercury-in-glass thermometer was used to take temperature readings. Biochemical Oxygen Demand (BOD) was determined using the 5-day dark bottle incubation method (APHA, 2005). Alkalinity was determined using the phenolphthalein titration method (APHA, 2005).

Estimating Cannibalism

The counting of surviving fish was carried out once every week, and during this count, the total length (mm) of all the survivors was quickly taken. Large fish with sizes greater than the cut-off length (Fish with length approximately greater than the sum of the current week’s mean length and the difference between the current week’s mean length and the preceding week’s mean length) were sorted out. Mortality was monitored daily (8:00 am), and dead fish were removed from each tank and recorded accordingly before being examined closely under a dissecting microscope to determine the cause of death. When collecting dead fish, mutilated dead fish and fish heads were recorded as type I cannibalism (Incomplete cannibalism). In contrast, fish that were unaccounted for were designated as fatality from type II cannibalism (Complete cannibalism) following the classification of Hecht and Appelbaum

(1988). The number of fish recorded for each type of cannibalism was converted to percentages. The rate of cannibalism was estimated from cumulative daily mortality as a result of cannibalism during the observation period (Hecht & Appelbaum, 1988) hence:

$$C_R = \sum_{n=15}^i M_c / n$$

Where C_R = Rate of Cannibalism; M_c = Mortality as a result of cannibalism, and n = number of days of observation.

Modelling Growth

Based on their low AIC (Akaike Information Criterion) values, the Gompertz model was the most suitable model for predicting growth in three crosses: Cl×Cl, Cl×Ht and HT×Cl. In contrast, the monomolecular model was the best fit for growth of progeny from the pure line cross of Ht×Ht. In all models, K = asymptotic length, r = growth constant and L_0 = minimum length.

The Gompertz growth model, as applied to length in the rate dL/dt form is:

$$rL \left(\ln \frac{K}{L} \right)$$

When this is transformed into length in time-based growth, it is parameterized as:

$$L_t = K \left(\frac{L_0}{K} \right)^{e^{-rt}}$$

When we used the log_e transformed lengths of the progeny in deriving the model, it yields the length (L) in time (t) form of the equation for growth in length for progeny from three of the crosses as:

$$L_t = e^{LnK(LnL_0/LnK)} e^{-Ln(r)*t}$$

The monomolecular growth model, as applied to length in the rate dL/dt form is:

$$r(K - L)$$

When this is transformed into length in time-based growth, it is parameterized as:

$$L_t = K - e^{-rt}(K - L_0)$$

When we used the \log_e transformed lengths of the progeny in deriving the model, it yields the length (L) in time (t) form of the equation for growth for progeny from the Ht×Ht cross as:

$$L_t = e^{LnK - e^{-Ln(r)*t}(LnK - LnL_0)}$$

The Absolute Growth Rate (AGR mm.day^{-1}) for the growth models fitted with the Gompertz equation was estimated using:

$$AGR (\text{mm. day}^{-1}) = e^{rKe^{-rt}(L_0/K)e^{-rt} \ln K/L_0}$$

While AGR for the growth model fitted with the monomolecular equation was estimated using:

$$AGR (\text{mm. day}^{-1}) = e^{re^{-rt}(K-L_0)}$$

Heterosis

Heterosis, the performance in each specified trait of cross breeds relative to the pure line cross, is expressed here in percentage. The estimation of heterosis was done using an adaptation of the formula by (Nguenga et al., 2000):

$$\% \text{ Heterosis} = \frac{[(M_1 + M_2)/2] - [(P_1 + P_2)/2]}{[(P_1 + P_2)/2]} \times 100$$

Where M_1 ; M_2 are mean values for trait of hybrids and P_1 and P_2 are for the pure line crosses.

Data Analysis

Data were analyzed using R version 3.4.3 (R Core Team, 2017). Descriptive statistics for length and cannibalism/mortality were obtained using Rmisc package in R (Hope, 2013) and reshape2 (Wickham,

2007). Differences in growth and cannibalism were determined using one-way ANOVA in R (R Core Team, 2017) via agricolae and emmeans packages (deMendiburu, 2017; Lenth, 2017). Mean separation was done using the Tukey HSD method implemented in multcomp package (Hothorn et al., 2008) and extracted using multcomp View (Graves et al., 2015). Differences in mean final length (MFL) were tested using analysis of covariance (ANCOVA). However, the mean initial length which was significantly different across the groups was not significant in determining MFL. Hence, a one-way ANOVA was used to determine differences in MFL. Graphical illustrations were done using the R package, ggplot2 (Wickham, 2016). Growth models were fit using the R package nlme version 3.1-137 (Pinheiro et al., 2018) with parameterization of the models according to Paine et al. (2012). Growth model selection was carried out through an R script so that the best model that fits the data was selected using the R^2 value and AIC (Akaike Information Criterion) as indicators. The R script was written to harmonize growth terms for each model type. Models included in the script were the exponential, gompertz and monomolecular models. Parameters extracted from the growth models include the asymptotic length K , growth rate r and L_0 (minimum length)

Results

Growth

The offspring's growth parameters (Table 3) indicate that the asymptotic length (K) of *H. longifilis* was higher than all other crosses, followed by the cross Cl×Ht. However, the decay in growth rate r (/day) was highest in Cl×Cl and lowest in Ht×Ht with equal r recorded for the reciprocal progeny. Therefore, the following equations define growth in length for progeny from each cross:

Cl×Cl: $L_t = e^{3.70(2.88/3.70)e^{-0.06*t}}$

Cl×Ht: $L_t = e^{4.08(2.97/4.08)e^{-0.02*t}}$

Ht×Cl: $L_t = e^{4.05(2.67/4.05)e^{-0.02*t}}$

Ht×Ht: $L_t = e^{4.28 - e^{-0.01*t}(4.28 - 2.55)}$

Table 3. Growth parameters of nonlinear growth modelling for the progeny of reciprocal crosses of *C. gariepinus* and *H. longifilis* reared in concrete tanks.

	K	$\text{Ln}K$	r	$\text{Ln}r$	L_0	$\text{Ln}L_0$
Cl×Cl	40.44	3.70	1.06	0.06	17.78	2.88
Cl×Ht	59.42	4.08	1.02	0.02	19.47	2.97
Ht×Cl	57.27	4.05	1.02	0.02	14.37	2.67
Ht×Ht	72.09	4.28	1.01	0.01	12.79	2.55

K = asymptotic length, r = growth rate decay constant and L_0 = minimum length.

The growth curves (Figure 1-4) were density dependent, with an increase in length over time as the survival rate declined. The point of intersection between the survival rate and the mean length of fish varied among the crosses. This point was highest in the cross Cl×Cl [Length (L)= 33 mm and survival (S)=78%] (Figure 1). The intersection point was similar in the reciprocal crosses (Figure 2 and 3): L=28 mm; S=58%; in the cross Ht×Ht (Figure 4), it was at L=25 cm and S=50%.

Cannibalism, Mortality, and Size Grading

The survival rates, mortality rate, and percentage of sorted-out individuals (Table 4) were not significantly different across the genetic groups or crosses ($p>0.05$). There was, however, a difference in the percentage of each type of cannibalism across the genetic groups ($p\leq 0.05$). Type I and type II cannibalism were more prevalent in Ht×Cl followed by Ht×Ht but least in Cl×Cl.

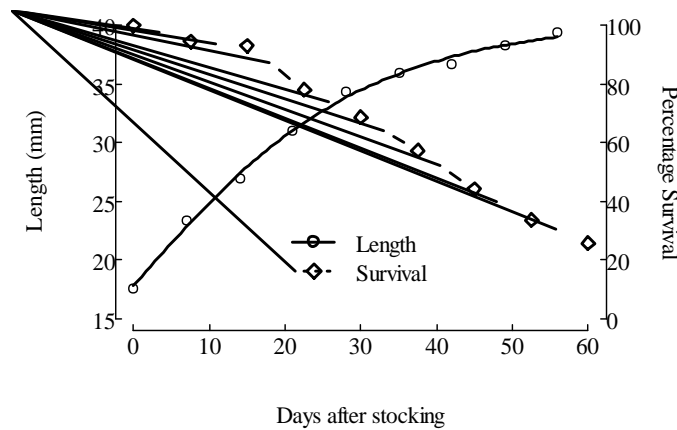


Figure 1. Growth curve (Gompertz model) and temporal survival of progeny from the cross Cl×Cl reared in concrete tanks.

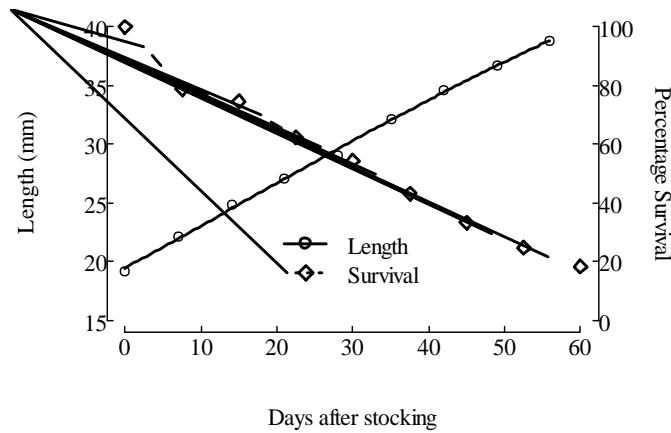


Figure 2. Growth curve (Gompertz model) and temporal survival of progeny from the cross Cl×Ht reared in concrete tanks

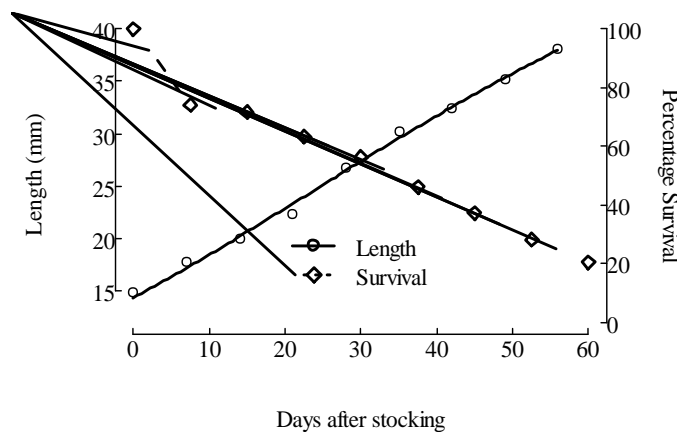


Figure 3. Growth curve (Gompertz model) and temporal survival of progeny from the cross Ht×Cl reared in concrete tanks.

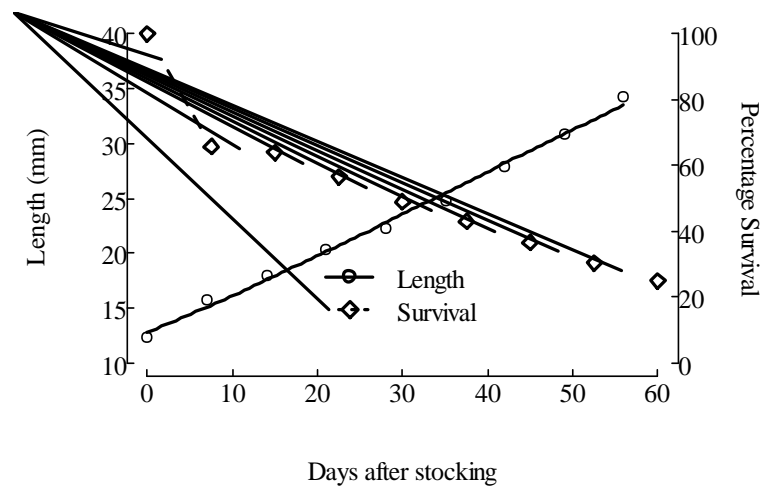


Figure 4. Growth curve (Monomolecular model) and temporal survival of progeny from the cross Ht×Ht reared in concrete tanks.

Table 4. Mortality and cannibalism in the progeny of reciprocal crosses between *C. gariepinus* and *H. longifilis* reared in concrete tanks

Cross	Survival (%)	Sorted (%)	Type I Cannibalism (%)	Type II Cannibalism (%)	Mortality (Other causes %)
Cl×Cl	73.67±7.51	52.67±5.46	6.67±1.45 ^b	2.33±0.33 ^b	17.33±5.78
Cl×Ht	63.67±4.26	49.33±4.91	7.33±0.33 ^{ab}	3.67±0.33 ^{ab}	25.33±3.84
Ht×Cl	55.33±0.33	39.33±2.19	11.67±1.2 ^a	5.33±0.33 ^a	27.67±1.33
Ht×Ht	57±5.69	37.67±1.45	9.67±0.88 ^{ab}	5.00±0.58 ^a	28.33±6.98
p-value	0.126	0.066	0.036	0.003	0.428

*Means in the same column followed by different superscripts differ significantly (p≤0.05).

The rate of cannibalism (Figure 5) indicates a steady increase from day 7 to day 21 and subsequent decline for the progeny of Cl×Cl, while the inflexion points for the decline in cannibalism for the cross Cl×Ht was at day 28. Cannibalism among the progeny of two crosses: Ht×Ht and Ht×Cl inflected at day 35, with cannibalism in both crosses being higher than the other crosses and the cross Ht×Cl had the highest rate of cannibalism over time.

Size and Growth Variation

There was a significant difference in mean initial length (MIL) between the genetic groups (Table 5), with progeny from Cl×Ht having the highest MIL and Ht×Ht having the least. Similarly, the coefficient of variation (COV) for initial length differed significantly (p≤0.05), with the cross Ht×Cl having the highest COV while Cl×Ht had the least. The absolute growth rate (AGR) also differed significantly, with Ht×Cl having the highest AGR for length and Ht×Ht having the least. There was no significant difference in mean final length (MFL) as well as COV of final length (p>0.05).

Temporal changes in the coefficient of variation for total length (Figure 6) show an initial spike in COV at week 1 for three crosses: Ht×Cl, Cl×Cl and Cl×Ht. A decline followed this over time. In contrast, the COV for the cross Ht×Ht undulated before increasing and

surpassing the other three crosses in week 6 but fell within the range of the others in week 8.

Heterosis for length was positive and high for MIL (Table 6) but declined by about 17% for MFL. The heterosis for absolute growth rate was high, suggesting that the cross breeds performed better than the pure line crosses by 16.3%. Heterosis for survival was negative as was that of sorting. This negative value suggests that the crossbreeds did not survive as well as the pure-line progeny. The sorting of large fish was superior for pure line progeny compared to cross breeds. Heterosis for type I and type II cannibalism was positive, indicating the transfer of traits of cannibalism from one or both of the pure-line parents.

Water Quality

The water quality parameters (Table 7) indicate conformity with recommended levels. The dissolved oxygen levels were ≥5.0 mg. l⁻¹ (≥80% saturation) and adequate for tropical freshwater fish (Mallya, 2007), while pH, which ranged from 7.72 to 7.78 was within 6.0 – 9.0 as recommended by Riffel et al. (2012). Total alkalinity was >20mg.l⁻¹ as Wurts (2002) recommended. Biological oxygen demand (BOD) is below the 5mg.l⁻¹ threshold as recommended by (Das, 1997) while the temperature was within the recommended range of 25–32°C (Das, 1997).

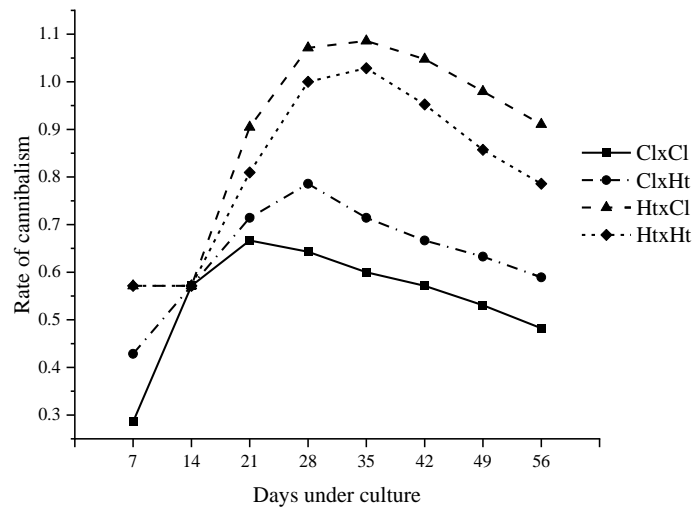


Figure 5. Intra-sibling cannibalism rate for fingerlings of reciprocal crosses between *C. gariepinus* and *H. longifilis*.

Table 5. Variation in total length and growth rate of the progeny from reciprocal crosses of *C. gariepinus* and *H. longifilis*.

Cross	MIL (mm)	MFL (mm)	COV L_0 (%)	COV L_1 (%)	AGR (mm.day ⁻¹)
ClxCl	18.00±0.20 ^{ab}	39.70±1.20	14.76±0.51 ^b	6.29±0.88	1.50±0.03 ^a
ClxHt	19.4±0.40 ^a	39.80±1.30	13.18±0.43 ^b	9.24±2.52	1.41±0.00 ^b
HtxCl	18.10±2.7 ^{ab}	38.90±1.70	20.09±1.93 ^a	8.43±1.51	1.52±0.00 ^a
HtxHt	12.7±0.30 ^b	35.20±1.40	13.58±0.95 ^b	9.22±0.69	1.02±0.00 ^c
p-value	0.037	0.154	0.009	0.536	0.000

*Means in the same column followed by different superscripts differ significantly ($p \leq 0.05$), COV (%) = Coefficient of variation [(Standard deviation/ Mean) × 100]; L_0 and L_1 = Initial and Final lengths respectively, AGR = Absolute Growth Rate.

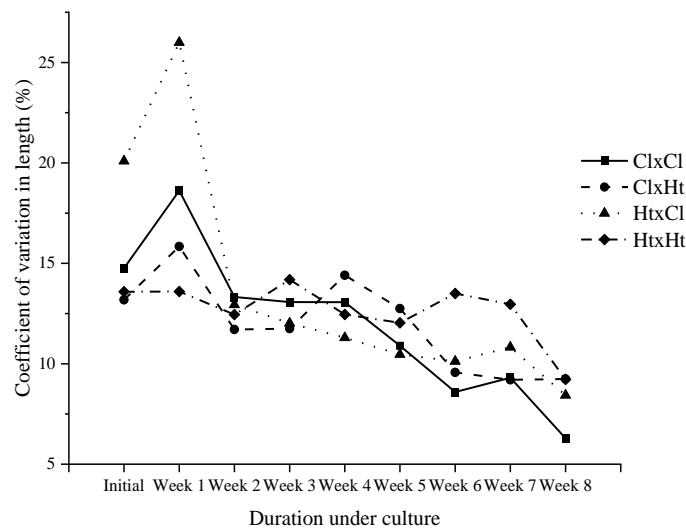


Figure 6. Temporal pattern in the coefficient of variation for total length in progeny from reciprocal crosses of *C. gariepinus* and *H. longifilis*.

Table 6. Estimates of heterosis of F1 progeny from crosses of *C. gariepinus* and *H. longifilis* reared in concrete tanks for 56 days.

Trait	Heterosis
MIL	22.15
MFL	5.07
AGR	16.27
Survival	-8.93
Sorting	-1.86
Type I Cannibalism	16.28
Type II Cannibalism	22.78

Table 7. Water quality indices in tanks used for rearing progeny of reciprocal crosses between *C. gariepinus* and *H. longifilis*.

Cross	pH	DO (mg.l ⁻¹)	Temperature (°C)	BOD (mg.l ⁻¹)	Alkalinity (mg.l ⁻¹)
Cl×Cl	7.73±0.1	5.77±0.18	30.58±0.38	3.55±0.08	23.12±0.14
Cl×Ht	7.78±0.1	5.75±0.18	30.30±0.41	3.39±0.07	23.01±0.20
Ht×Cl	7.72±0.1	5.56±0.20	30.32±0.34	3.43±0.06	23.14±0.19
Ht×Ht	7.78±0.1	5.77±0.17	30.29±0.41	3.47±0.08	23.30±0.24

Discussion

The Gompertz and monomolecular models successfully converged to describe growth for the different crosses evaluated; hence the parameters of the functions can be used to estimate the growth and maturity of the fish. Growth model fitting and adjustment is the initial step in determining the nutritional requirements of various animal genotypes and allowing such animals to be selected for a breeding plan (Gous et al., 1999). The asymptotic lengths indicate that the cross Cl×Cl has approached the growth limit within the system, and further rearing within the system at the terminal density would produce stunted fish. Practically, this tends to be unrealistic as Mortality ensures a reduction in space that shifts the asymptote higher hence the feeling of growth that will be experienced. The cross Ht×Ht, however, is just about 50% of its asymptotic length at the end of the trials. This length indicates that although the progeny has a slow growth rate, they will attain a larger size than progeny from other crosses. The reason behind the cross Cl×Cl approaching its asymptotic length can be seen clearly from the intersection of the growth curve and the survival curve. Progeny from the pure line *C. gariepinus* cross have grown fast even under high density such that at >70% survival, mean length intersected survival while other crosses had the intersection at lower survival percentages. Therefore, Cl×Cl can tolerate high stocking density (Oké & Goosen, 2019). The trait for fast growth at high density seems to be linked to maternal and paternal lines in *C. gariepinus*. This linkage should explain why the reciprocal crosses had higher intersection levels than the pure line *H. longifilis* cross.

In this current study, type I cannibalism (incomplete cannibalism) was more than type II cannibalism among all crosses. The pattern of type I cannibalism was such that similar-sized fish attacked a smaller and weaker individual, nibbling on it until it succumbs to mortality. The left-over carcasses were used as data points for this type of cannibalism. In type II cannibalism, a larger fish swallows a smaller one whole and acquires a weight that can be misleading when growth by weight is measured. This is the core reason we used length to measure growth. Moreover, the allometric growth function (Jones 2009) does an excellent job in transforming growth between length form and weight form and vice versa.

The difference in type I and type II cannibalism across the genetic crosses indicates a well-known pattern in the African catfishes. It is clear that in crosses

where *H. longifilis* was involved as the sire and/or dam, there was a high incidence of type I cannibalism. This involvement shows the already established omnivorous (Temenu, 2014) and voracious (Ajah, 2010) nature of *Heterobranchus* sp. In addition, the earlier knowledge on causes of cannibalism shows that size heterogeneity (Barton et al., 2002; Naumowicz et al., 2017) that elicits hierarchy and dominance was a leading cause, but the availability of food considering quantity and frequency can also be a factor (Reddy et al., 1995). While the element of size heterogeneity was not controllable in the current study, feed availability was ensured through *ad libitum* feeding. Therefore, lack of feed cannot be a basis for aggressive tendencies leading to cannibalism. The rate of cannibalism is directly linked to the level of aggressiveness. The higher rate of cannibalism throughout culture in the progeny of the crosses: Ht×Ht and Ht×Cl is therefore linked to aggressiveness. Aggressiveness was characterized by vicious chasing and biting/nibbling on the victims, resulting in skin lesions with accompanying haemorrhage. The use of energy in aggression is also a factor contributing to a decline in growth (Hecht & Uys, 1997) through mortality, high feed conversion ratio and delayed growth. The effect of sorting on the performance of the African catfish is usually increased yield and uniformity in size (Mun et al., 2019; Nightingale et al., 2018). The sorting of larger individuals in this trial contributed to the recorded overall survival.

The difference in MIL across the genetic groups is a phenomenon that occurs in the early ontogeny of organisms (Huss et al., 2007). Although the MIL for the pure line crosses were not significantly different, there seems to be a genetic effect of the crossbreeding on the MIL such that the sires conferred some growth-boosting phenotype to the offspring in the reciprocal crosses. The effect of these differences is seen in the coefficient of variation for initial length. The uniformity in length at the end of the trial indicates the advantage of sorting to growth homogeneity. The mechanism behind growth modulation by fish sorting has led to various theories, including competition for food (Ward et al., 2006), stress response (Brown et al., 2005) and disparity in vigour (Wieser, 1995). The size of intra-cohort individuals will surely affect their ability to pick up aggressive behaviour. This size-dependent behaviour is why the final survival rate was least in the cross Ht×Cl given its greater COV at the start of the trial and a high rate of cannibalism throughout the trial.

Hybrid vigour (Heterosis) is the main goal behind crossbreeding, and it is evaluated as a metric to trace

outbreeding and identify better progeny (Jothilakshmanan & Marx, 2013). When we look at the growth rates of the progenies for each group, it is clear that crossbreeding has a genetic effect on growth with *C. gariepinus* sire and dam contributing to improved growth in combination with *H. longifilis* dam and sire respectively. The current research has made the first attempt to estimate heterosis for sorting and cannibalism. Sorting out larger fish from the tank was more effective in the pure line crosses than the cross breeds. Hence, the criterion for sorting is more effective on the pure line progeny than the hybrids. Heterosis for cannibalism means that the hybrids obtained superior cannibalistic tendencies from their parents (Solomon & Udoji, 2011). When this is coupled with the difficulty in sorting out larger individuals from the cohort, it effectively explains the low survival rate recorded for the hybrids. These notwithstanding, the heterosis for growth obviously is the fuel for spontaneity in large-size fish within the hybrid progeny, a situation that was elusive when progeny from these crosses were reared in plastic aquaria (Ataguba et al., 2010).

In conclusion, the growth pattern in linear terms for crosses of the two African catfishes clearly shows that *H. longifilis* has the potential to grow larger than *C. gariepinus*, with growth being density-dependent. Secondly, crossbreeding of the catfishes led to a greater asymptotic length than in pure line *C. gariepinus* suggesting the conferment of growth phenotype from *H. longifilis* on the resulting offspring. Cannibalism is high when there is a genotype contributed from *H. longifilis*. Crossbreeding of the two African catfish species produced heterosis for linear growth and absolute growth rate for length. Sorting of larger fish effectively reduced coefficient of variation for length. For farmers who are culturing the hybrid catfish, it is recommended that sorting be carried out at intervals ideal to the farmer and that feeding be done correctly to avoid size heterogeneity and its attendant consequence of cannibalism. Finally, this research has produced models that can accurately predict the carrying capacity of culture systems in terms of the maximum length the fish can attain in the system under the prevailing density. This information is useful for stocking and management of the farm.

Ethical Statement

This research was conducted based on the enabling legal provisions captured in the Constitution of the Federal Republic of Nigeria, Criminal Code Act. Cap C38 LFN 2004, Animal Diseases (Control) Act. Cap A17 LFN, 2004 and the Veterinary Surgeon Act Cap V3 LFN 2004. The protocol was approved by the Animal use and care committee of the College of Veterinary Medicine, Federal University of Agriculture, Makurdi, Nigeria via document No. nvriAUCC F001/15. Fish lengths were measured while submerged in a little quantity of water before being returned to the tanks.

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Author Contribution

Conceptualization: GAA, PAA, AAG; Data Curation: GAA; Formal Analysis: GAA, AAG; Fund acquisition: GAA, PAA, AAG; Investigation: GAA; Methodology: GAA, PAA, AAG; Supervision: PAA; Validation: PAA; Writing (Draft): GAA, AAG; Writing (Review): PAA, GAA

Conflict of Interest

The authors have no conflict of interest to declare.

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